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Food supplementation does not increase demographic rates in a passerine species of conservation concern

Innes M.W. Sim[1], Nicholas I. Wilkinson[1], Davide Scridel[2,4], David Anderson[3,4], Staffan Roos[1]

1 *RSPB Centre for Conservation Science, RSPB Scotland, 2 Lochside View, Edinburgh Park, Edinburgh, EH12 9DH* **2** *Imperial College London, Silwood Park Campus, Ascot, Berkshire, SL5 7PY, UK* **3** *Edinburgh Napier University, 10 Colinton Road, Edinburgh, EH10 5DT, UK* **4** *Present address: Royal Society for the Protection of Birds (RSPB) Scotland, 2 Lochside View, Edinburgh Park, Edinburgh, EH12 9DH, UK.*

Corresponding author: *Innes M.W. Sim* (innes.sim@rspb.org.uk)

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Abstract

Numerous studies have examined the effects of the provision of supplementary food on aspects of avian reproductive success, but far fewer have gone on to examine the potential positive effects of food supplementation on the demographic rates which are key for population growth rate. Testing for potential effects of food shortage on vital rates is likely to be particularly important in species of high conservation concern, where populations are particularly small, isolated or decreasing rapidly. Here we test the effects of the provision of supplementary food on reproductive success, body condition at fledging and post-fledging survival of ring ouzels (*Turdus torquatus*), a species of high conservation concern in the UK. However, food supplementation had no detectable effect on any of these parameters. There was no significant difference in return rates of fed and unfed fledglings in the year following hatching, and most post-fledging mortality was apparently caused by predation by raptors and mustelids. We conclude that the supply of invertebrate food sources for nestlings was not a major limiting factor in our study area, at least during this two-year study. Further studies are required to quantify the precise mix of habitats used by ring ouzels, at the appropriate scale, which provide concealment from predators and access to food supplies throughout the spring and summer months.

Keywords

Food supplementation, demographic rates, passerine species, conservation

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Introduction

The provision of supplementary food has been trialled as a method for increasing reproductive success and/or survival in a range of avian species, especially those of conservation concern where populations are particularly small, isolated or decreasing rapidly (e.g. Armstrong et al. 2007; Houston et al. 2007; Schoech et al. 2008). However, such trials have had mixed success, with some showing apparent positive impacts of food supplementation, and others showing mixed or uncertain results. For example, supplementary feeding increased kakapo (*Strigops habroptilus*) and hihi (*Notiomystis cincta*) reproductive success, through improved nestling survival to fledging (Elliott et al. 2001; Walker et al. 2013). However, food supplementation did not result in increased survival of adult bearded vultures (*Gypaetus barbatus*), despite increasing the survival of pre-adults, and did not influence adult or fledgling survival in barn owls (*Tyto alba*) (Meek et al. 2003; Oro et al. 2008). Thus, further data on the effects of food supplementation on avian reproductive success and survival, especially in species of conservation concern, is desirable.

Since providing supplementary food can be a costly and labour-intensive conservation management action, it is important that there is clear evidence for food shortage before feeding begins. For example, in the New Zealand hihi, providing supplementary food increased abundance and survival of translocated birds on Kapiti Island, following evidence that food was limiting on previous island translocations (Chauvenet et al. 2012). It is also important that the life-history stage(s) which are most likely to influence population growth rate (λ) of the study population are targeted for conservation action. For instance, numerous studies have shown that avian λ is more heavily influenced by first year and adult survival than by reproductive success (e.g. Sæther and Bakke 2000; Reid et al. 2004; Schaub et al. 2006). Thus, there would be little purpose in providing supplementary food to increase reproductive success, if this demographic rate was predicted to have little impact upon λ in the target species.

The ring ouzel, hereafter 'ouzel', is a species of high conservation concern in the UK (Eaton et al. 2011). Declines of this migratory, typically double-brooded, upland thrush species are widespread throughout the UK, but the underlying mechanisms are poorly understood (Sim et al. 2010). However, in a study population in Scotland, a decline in brood size at fledging of successful early season nests during 1998-2009 suggested that poor food supply to nestlings may have reduced survival from hatching to fledging (Sim et al. 2011). In addition, post-fledging survival was higher for individuals fledging from broods earlier in the season, although there was also support for models which included a positive effect of body condition on post-fledging survival (Sim et al. 2013b). Thus, reduced body condition at fledging may have been caused by food shortage, resulting in lower survival during the post-fledging period. Ouzel nestlings are fed mainly on earthworms (*Lumbricidae*), larval leatherjackets (*Tipulidae*) and ground beetles (*Coleoptera*) (Burfield 2002), and it is likely that the abundance of these invertebrate groups has declined in the UK uplands in recent decades due to changes in moorland management, such as intensification of heather burning and increased ditch construction, which might affect soil conditions, vegetation structure and com-

position (Dennis et al. 1998; Buchanan et al. 2006; Evans et al. 2006). Therefore, ouzel declines may be linked to declines in the abundance of key invertebrate prey.

A recent demographic analysis of one ouzel study population indicated that λ was most sensitive to apparent first-year survival (fledging to age one year), closely followed by re-nesting rate and early-season reproductive success, and that first-year survival contributed most to observed variation in λ (Sim et al. 2011). Additionally, most (63–68%) estimated first-year mortality occurred in the first five weeks post-fledging, indicating that low juvenile survival through this specific period may substantially affect λ (Sim et al. 2011). Therefore, conservationists would be most likely to improve ouzel λ by implementing measures that increase reproductive success and post-fledging survival.

In this paper we report the results of a two-year field experiment in which we provided supplementary food to a declining population of ouzels, in an attempt to improve their reproductive success and post-fledging survival. We hypothesised that adult provisioning rates to nestlings, fledging success, brood size at fledging, nestling body condition at fledging and post-fledging survival would all be higher, and within-brood variation in nestling body condition would be lower, in fed than in control territories, where no supplementary food was provided.

Methods

Study area and species

The ring ouzel is a medium-sized migratory thrush that breeds in north-west and central Europe and winters in southern Spain and North Africa (Wernham et al. 2002). We studied a population in Glen Clunie (56°56'N, 3°25'W; 18 km^2), north-east Scotland during 2011–12, that has been part of a long-term study since 1998 (Sim et al. 2011). An additional area of approximately 8 km^2 in the adjacent Glen Callater (56°57'N, 3°22'W) was included in the study in 2011 only. The vegetation in the upper slopes of these glens is a mosaic of heathers (*Ericaceae*), bilberry (*Vaccinium myrtillus*), crowberry (*Empetrum nigrum*) and rough grassland, interspersed with numerous crags, scree slopes and gullies, and improved grassland and small conifer plantations in the valley floors. The area is managed for sport shooting of red grouse (*Lagopus lagopus scoticus*) and red deer (*Cervus elaphus*), largely through heather burning, used to provide a mosaic of vegetation structure thought to benefit red grouse. The area is also grazed by sheep and cattle at low densities. Gamekeepers legally and effectively eliminated generalist predators such as red fox (*Vulpes vulpes*) and carrion crow (*Corvus corone*), but we regularly observed stoats (*Mustela ermine*) and weasels (*M. nivalis*).

In each year we aimed to locate all ouzel breeding pairs and nesting attempts. The study area was systematically surveyed, by walking all ground to within 200 m of observers, every one to two weeks between mid-April and mid-July (Sim et al. 2011). Ouzels vigorously defend the immediate vicinity of nests, but disputes outside this area are rare (Burfield 2002). A successful breeding cycle requires 29-30 days (16-17 days for egg laying/incubation plus 13 days until fledging; Burfield 2002), and Brit-

ish ouzels regularly make two, rarely three, breeding attempts per season (Sim et al. 2012). The number of 'early' and 'late' pairs were defined as those laying eggs within 30 days of the first laying date recorded in the population, and on or after day 31, respectively, in each year (Sim et al. 2011). Egg laying date was recorded directly in nests found during laying or hatching, estimated using known relationships between chick age and wing-length and mass (Burfield 2002) or by comparison with photographs of known-age nestlings. We visited nests every 3–5 days to record potential breeding failures, to count the number of eggs and hatched chicks, and to measure the mass and wing length of chicks. During 2011–12, we located 69 early and 49 late nests before nestlings fledged, comprising 93% and 98% of known successful early and late nests, respectively. We located 77% of nests with eggs and 23% with nestlings.

To allow individual identification, 263 nestlings (145 from early and 118 from late nests), comprising 90% of individuals known to fledge in the study area, were ringed with BTO metal rings and individual combinations of three plastic colour rings. In addition, 17 (2011) and 29 (2012) individually colour ringed adults marked previously in the study area as either breeding adults or nestlings returned to breed, and a further 12 (2011) and 24 (2012) adults were caught and colour ringed.

Experimental design

In 2011, we randomly allocated 50% of the known territories (i.e. those occupied at least once between 1998 and 2010; N_{total} = 86) to receive supplementary food for both early and late breeding attempts ('fed' territories). The remaining 50% of the known territories were 'control' territories, where no supplementary feeding occurred. In 2012, we reversed treatments, so that control territories from 2011 became fed territories, and vice versa. In both years our aim was to have approximately equal numbers of fed and control territories. However, this 'ideal' experimental design was not possible in territories that were occupied only in either 2011 or 2012, in those territories where ouzels did not find or utilise the supplementary food, or where feeding had to be abandoned before nestlings fledged due to other species taking the supplementary food (see Results for details). When feeding was not possible in a planned fed territory, the next occupied territory on the 'fed' random list was selected to receive supplementary food. Thus, despite our ambitions, we ended up with an unbalanced experimental design in terms of numbers of fed and control territories across the two years.

Food supplementation

Supplementary food was provided during the ouzel nestling-rearing stage in black plastic seed trays (38 cm × 24 cm × 6 cm) placed on prominent knolls, boulders or in short grass-rich areas on the ground, between 20 m and 50 m from ouzel nests. These locations were chosen to make the food as obvious as possible to the ouzels, while reducing the risk of

predators locating the nest. We observed these feeding trays to determine (a) if the ouzels and/or other species fed from them and (b) what food source [live earthworms (*Dendrobaena* spp.), or live mealworms i.e. the larvae of the mealworm beetle (*Tenebrio molitor*)] was preferred. In 2011, we provided 100 g of both earthworms and mealworms in each territory daily, in order to replicate the key natural food sources of nestling ouzels. Mealworms have a relatively high protein (45–60%) and fat (30–45%) content (Bernard et al. 1997; Tran et al. 2013), similar to that found in beetle larvae (protein 23–66%; fat 9–67%; Banjo et al. 2006; Van Huis et al. 2013), and we therefore assumed that they provided a suitable partial food source for nestling ouzels. However, since only 5 of 13 (38%) ouzel pairs selected earthworms in 2011 and these escaped relatively easily from the feeding trays, thus becoming unavailable to ouzels, only 100 g of mealworms was provided daily in 2012. Mealworms were regularly taken by ouzels, and since they were unable to escape from the trays they were available for longer periods. At a single territory, we observed a male ouzel from a control territory taking supplementary food from the neighbouring fed territory. Feeding trays were only very rarely completely empty when they were re-visited to replenish them with mealworms (i.e. we effectively provided supplementary food *ad libitum*).

Provisioning rates

We monitored adult provisioning rates to nestlings at fed and control sites using x10 binoculars or ×15–40 zoom telescopes, from hides, cars, or by observers well concealed in open moorland, at distances of 30–200 m from nests, depending on topography and the sensitivity of the adults to disturbance. Each provisioning watch lasted for 60 minutes, and we classified food brought to the nest as supplementary (earthworms or mealworms taken from the feeding trays) or natural (gathered away from the feeding trays and therefore assumed to be natural). In 2011, we carried out 1–2 (mean 1.25 ± 0.11) watches at control nests when nestlings were aged 7–12 (mean 9.37 ± 0.33) days old, and 1–8 (mean 2.60 ± 0.22) watches at fed nests when nestlings were aged 5–13 (mean 9.26 ± 0.25) days old. In 2012, we carried out 1–3 watches at control (mean 1.97 ± 0.10) and fed (mean 1.95 ± 0.10) nests when nestlings were aged 4–12 (mean; control 8.16 ± 0.30: fed 7.94 ± 0.31) days old.

Body condition at fledging

To test whether within-brood variation, and individual nestling body condition, at fledging varied between fed and control nests, we measured body condition index (BCI) as the residual of a regression of body mass on wing length^3 (body mass = 66.2 + 0.00001* wing length^3; r^2_{adj} = 0.05; Genevois and Bretagnolle 1994). We measured wing length (maximum chord to the nearest 1 mm) and body mass (to the nearest 0.5 g, using a Pesola balance) for all nestlings aged 10–14 (mean for control and treatment nestlings = 12) days post-hatch (Burfield 2002).

Juvenile post-fledging survival and return rates

To measure survival during the post-fledging period, we fitted nestlings with 1.8 g TW4 single-celled radio transmitters (Biotrack 2013) just prior to fledging (10–14 days post-hatch), at which age we also recorded brood size (the number of nestlings alive). Transmitters were thigh-mounted using a silastic (pliable plastic) harness with a weak cotton link, to allow tag loss prior to migration (Hill et al. 1999; Rappole and Tipton 1991). In 2011, we fitted transmitters to 11 fed and 25 control nestlings from early broods, and 14 fed and 16 control nestlings from late broods. In 2012, we fitted transmitters to 17 fed and 23 control nestlings from early broods, and 19 fed and 18 control nestlings from late broods. Individuals fitted with transmitters appeared to fly as well as juveniles without transmitters when flushed, and dispersed over similar distances and time periods as colour ringed siblings. They thus showed no detrimental behavioural effects of radio transmitters, in common with previous studies (Rae et al. 2009; Gow et al. 2011; Sim et al. 2013b). We aimed to fit transmitters to at least one nestling from all successful broods. Each nestling in the two broods with a single nestling were fitted with transmitters. In the remaining 77 broods of 2–5, nestlings were ranked according to maximum chord wing length (the best predictor of nestling age; Burfield 2002), and 1–3 nestlings were selected at random according to these rankings, and fitted with transmitters. Thus, transmitters were fitted to single nestlings in 17 broods of 1–4, two nestlings in 57 broods of 2–5 and three nestlings in four broods of 5.

We tracked juveniles with transmitters and recorded their approximate locations every 3–4 days post-fledging, until the individual was found dead, shed the transmitter, or disappeared and was assumed to have dispersed from the study area. Individuals were tracked at different times on different days. Transmitters had signal ranges of approximately 10 km when in direct line of sight, but more typically 2–3 km depending on terrain, and a battery life of 3–4 months. We used Advanced Telemetry Systems (ATS) scanning receivers attached to car roof-mounted aerials to provide approximate locations. Hand-held Telonics TR-4 receivers, attached to three-element Yagi antennas, were used to visually locate each individual on foot, and record their location using a Garmin Global Positioning System (GPS) 12 Personal Navigator. In addition, we recorded the observed return rates of individually colour-ringed nestlings from fed and control nests in the years following ringing.

Causes and timing of mortality

We examined remains of dead juveniles to determine the most likely cause of death. Individuals found in raptor nests or elsewhere with plucked feathers and bent radio-tag aerials were assumed to have been eaten and most likely killed by raptors, whereas those located underground in tunnels, under boulders, or in the open with bitten feathers and straight aerials were assumed to have been eaten and most likely killed by mammals (Thirgood et al. 1998). We assumed that juveniles with no apparent injuries

found close to their nest soon after fledging had died from starvation or exposure. Because juvenile location and status (dead/alive) were checked at 3–4 day intervals, the timing of mortality was also accurate to within 3–4 days.

Statistical analysis

We were primarily interested in the level of support for supplementary feeding on ouzel fledging success (the proportion of hatched nestlings that fledged, excluding nests which failed to fledge any young since these were almost certainly predated), brood size at fledging (again excluding nests which failed to fledge any young), nestling BCI at fledging (both for individual nestlings and within-brood variation in nestling BCI, the latter measured as the standard deviation of brood BCI) and post-fledging survival, compared to control territories (0 days feeding). However, since there was considerable variation in the number of days that nestlings received supplementary food (hereafter 'feeding days'; see Results for details), we used feeding days as a predictor variable in all analyses, rather than the binary predictor fed/control.

We used Generalised Linear Models (GLMs; in the base package in R; R core team 2013), and Generalised Linear Mixed Models (GLMMs; in the LME4 package in R (Bates et al. 2014) to assess the level of support for models predicting adult provisioning rate to nestlings, fledging success and brood size and BCI at fledging. Akaike's Information Criterion, adjusted for small sample size (AICc), was used to identify the best supported model that included the parameters of interest (Burnham and Anderson 2002). The model with the lowest AICc is the best supported model, and provides the best fit to the data of the models compared (Burnham and Anderson 2002). We examined models with ΔAICc values of ≤ 2.0 to see if they differed from the best supported model by one parameter, and had essentially the same values of maximised log-likelihood as this model. In such cases, the larger model is not really supported since it is 'close' only because it adds one parameter to the top ranked model and therefore will be within 2 ΔAICc units of it (Burnham and Anderson 2002; Arnold 2010). Similar caveats were applied to models with two extra parameters that fell within approximately 4 ΔAICc units of the best supported model. In general, we included only those variables which previous studies have found to influence ouzel reproductive success, such as brood (early or late), hatch date and fledge brood size (Burfield 2001; Sim et al. 2011). Year was included as a nuisance factor in all models. Following recommendations by Burnham and Anderson (2002), we constructed biologically plausible models with as few explanatory variables as possible to avoid over-parameterization. This meant that we did not run all possible permutations of the global model. In addition, due to relatively low sample size, we included only those 2-way interactions for factors considered to influence ouzel breeding success from the literature. Finally, we did not implement model averaging when two or more competing models had similar levels of support (AICc < 2.0), as the presence of any 2-way interactions makes the interpretation of model averaging problematic (Grueber et al. 2011). We first measured the rela-

tive support for models predicting provisioning rate, fledging success, and brood size and BCI at fledging that included univariate effects of brood (early or late), hatch date and hatch date^2, which were highly correlated (Spearman rank correlation between brood and hatch date $r = 0.86$, $p < 0.0001$). In all models, brood received the strongest support, so hatch date and hatch date^2 were omitted from further analyses. For the provisioning rate model, we tested for effects of factors year and brood, and covariates feeding days, brood size and nestling age on their own, when added to one another and including all possible two-way interactions. This process was repeated for the fledging success (excluding nestling age and brood size), brood size at fledging (excluding nestling age and brood size, but including brood size at hatching) and BCI at fledging (excluding nestling age) models. We modelled fledging success and brood size at fledging using a binomial error structure with a logit link function, and a Poisson error structure with a log link function, respectively. For adult provisioning rate to nestlings, individual nestling BCI at fledging and within-brood variation of nestling BCI, we used a normal error structure with an identity link function. For the adult provisioning rate to nestlings, and individual nestling BCI at fledging models, we accounted for multiple measures of nestling BCI, and multiple provisioning watches, from within the same territory by specifying territory ID as a random factor in the GLMM.

We ran juvenile survival analyses over 100 days post-fledging (25 × 4-day periods), after which no individuals fitted with radiotransmitters remained within the study area, using the known-fate model in program MARK 5.1 (White and Burnham 1999). A goodness-of-fit test is not necessary for known-fate models, since the saturated model by definition fits the data perfectly (Cooch and White 2008). Known-fate models assume (a) that the fate of each individual is known with certainty (although 'missing' individuals can be censored during the period they are not found, and re-enter the dataset when they are relocated) and (b) that the fates of individuals are independent. When individual survival probabilities are not independent, estimated effects are unbiased, but variances are biased downward because of extra-binomial variation or overdispersion of the data (Tsia et al. 1999). Biologically, overdispersion might be expected if the fates of different brood members covary. We tested for significant violation of the assumption of independence by estimating overdispersion ($\hat{c}$) as χ^2/df, where χ^2 is the summation of partial chi-square values ([observed - expected]^2/[expected]) calculated for each possible outcome of losses within tagged brood sizes of one, two, or three young (nine possible outcomes). Expected values were calculated as: $(n/r)\varphi^r(1-\varphi)^{n-r}$, where n is brood size, r is the number of young surviving to independence, and φ is the survival rate between fledging and independence (Wiens et al. 2006). There was no evidence of overdispersion ($\chi^2 = 7.26$, $df = 8$, $p = 0.51$), and individual fates were therefore treated as independent. Twenty-seven individuals were temporarily censored for up to 13 consecutive four-day periods for which they were unobserved before being relocated.

Using AICc, we first tested the relative support for models where survival was constant or varied across all 25 four-day periods. We then tested for effects on survival of the factors year and brood, and covariates BCI, brood size and feeding days on their own, when added to one another and including all possible two-way interactions.

Results

Food supplementation

The proportion of ouzel pairs in fed territories that we observed feeding the supplementary food to their nestlings did not differ between 2011 (13/19, 68%) and 2012 (16/18, 89%: $\chi^2 = 2.29$, $p = 0.13$). However, nestlings received supplementary food for a longer period in 2012 (mean 10.69 ± 0.42, range 8–12 days) than in 2011 (mean 6.23 ± 0.51, range 4–9 days; $t = 6.54$, $df = 25$, $p < 0.0001$). Wheatears (*Oenanthe oenanthe*) and meadow pipits (*Anthus pratensis*) occasionally 'stole' the supplied food, but were quickly chased off by ouzels and were considered to have a negligible impact upon the amount available to ouzels. Common gulls (*Larus canus*) located the food at two territories after 3–6 days of feeding in 2011, and at six territories after 3–8 days of feeding in 2012, and rapidly emptied the trays. We then ceased the food supplementation in these territories, since no food was available for ouzels and because of the increased risk of predation of ouzel nestlings by common gulls. Such territories were subsequently removed from the experiment, since they could not be reliably categorised as either fed or control. We re-classified the six (2011) and two (2012) territories where we provided food, but never observed it being taken by ouzels, as controls. Thus, during 2011–12, we successfully provided supplementary food at 21 territories, with a further 34 territories classed as controls.

Provisioning rates

We carried out provisioning rate observations, by adults to nestlings, at 5 of 13 (38%) early, and 9 of 16 (56%) late, control territories, and at 7 of 11 (64%) early, and 8 of 9 (89%) late, fed territories in 2011. In 2012, observations were carried out at all early ($n = 16$) and late ($n = 9$) control territories, and at 12/13 (92%) early, and at all 11 late, fed territories. Supplementary food was supplied in 538/740 (73%) of deliveries to nestlings by adults at fed nests. In addition, adults were observed eating the supplementary food at 9/12 (75%) of fed territories in 2011, and at 15/17 (88%) of fed territories in 2012.

The best supported model for provisioning rate included the added positive effects of nestling age and year (Suppl. material 1: Table S1). Although the second best supported model had a ΔAICc value of 1.4, it contained one additional parameter and the same covariates as the best supported model, and was therefore not considered competitive.

Reproductive success

Reproductive success results are summarised in Table 1. There was no significant difference in early nest mean clutch size between fed and control territories in either 2011 ($t = 1.74$,

Table 1. Ring ouzel reproductive success parameters measured for early and late broods at all fed and control nests during 2011–12. Figures presented are means ± s.e., with sample size given in parentheses. Data for mean clutch size in late nests comes only from individually identifiable colour ringed females.

Variable	2011 fed	2011 control	2012 fed	2012 control
Number of early territories	9	14	10	17
Number of late territories	7	16	8	10
Mean clutch size in early nests	4.11 ± 0.11 (9)	3.85 ± 0.10 (13)	4.08 ± 0.08 (12)	3.86 ± 0.10 (14)
Mean clutch size in late nests	5.00 ± 0.00 (2)	4.00 ± 0.31 (5)	4.00 ± 0.26 (6)	4.00 ± 0.32 (5)
Early brood fledging success	0.74 (9)	0.84 (14)	0.89 (10)	0.85 (17)
Late brood fledging success	0.74 (7)	0.87 (16)	0.87 (8)	0.70 (10)
Mean brood size at fledging in successful early nests	3.25 ± 0.37 (8)	3.07 ± 0.20 (14)	3.78 ± 0.22 (9)	3.31 ± 0.27 (16)
Mean brood size at fledging in successful late nests	4.00 ± 0.55 (5)	3.86 ± 0.21 (14)	3.71 ± 0.36 (7)	3.71 ± 0.18 (7)

$p = 0.10$) or 2012 ($t = 1.77$, $p = 0.09$), and thus no evidence of differences in territory and/or adult quality between treatment groups before supplementary feeding commenced. The top five best supported models predicting fledging success all indicated higher success for late broods compared to early broods (Suppl. material 1: Table S2). Since the brood-only model was only 1.5 ΔAICc units higher than the top-ranked model, which contained an extra parameter (year), we conclude that increased fledging success was largely associated with late broods. The top seven best supported models predicting brood size at fledging in successful nests indicated that brood size at fledging was largely determined by brood size at hatching, and the best supported model contained only this parameter (Suppl. material 1: Table S3).

BCI at fledging

Since the null model predicting individual nestling BCI at fledging received almost as much support as the two top-ranked models, we conclude that none of the models successfully predicted nestling BCI at fledging (Suppl. material 1: Table S4). The top three best supported models predicting within brood variation in nestling BCI indicated that variation was positively associated with larger broods (Suppl. material 1: Table S5). The addition of brood as a covariate, and as an interaction with brood size, added little additional support for these two models.

Juvenile post-fledging survival and return rates

The model with the highest support regarding juvenile survival for up to 100 days post-fledging indicated a positive association with BCI at fledging (Suppl. material 1: Table S6, Fig.1). The next three highest-ranked models (ΔAICc = 0.7–2.0) also contained BCI at fledging, plus between one and three additional parameters, including

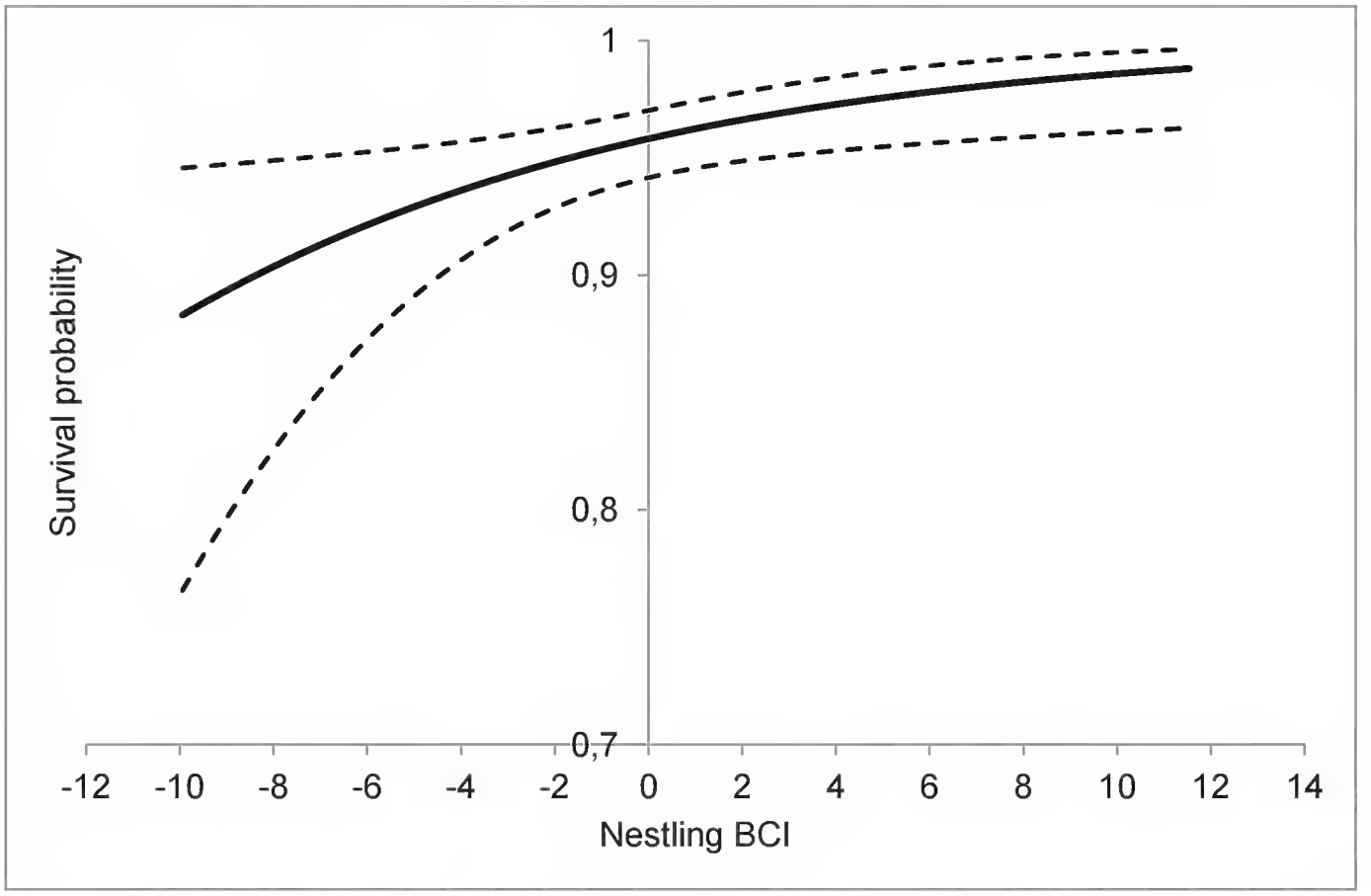

Figure 1. Predicted relationship between 4-day survival probability (solid line), ± 95% C.I. (dashed lines) and nestling body condition index (BCI) for ring ouzels in Glen Clunie during 2011–12.

the second-ranked model which indicated a positive additive effect of the provision of supplementary food. However, since these three models all lay within 2.0 AICc values of the best supported model, and contained between one and three extra parameters, they were not considered competitive to the best supported model. There was no significant difference between treatment groups in the proportion of colour ringed nestlings that were observed returning to the study area in the years following ringing (pooling data across 2011 and 2012: control 13/152; 0.09: fed 6/117; 0.05: $\chi^2 = 1.18$, $p = 0.28$).

Causes and timing of mortality

Of the 143 juveniles fitted with transmitters, 60 (42.0%) could no longer be tracked 20–84 days after fledging and were assumed to have dispersed outside the study area, 40 (28.0%) were found dead, 35 (24.5%) shed their transmitters within the study area, and a single (0.7%) transmitter was known to have stopped working prematurely (the individual could still be identified by individual colour rings). A further seven (4.8%) transmitters were assumed to have stopped working within 16 days of fledging, since their signals became increasingly weak and intermittent in the days preceding their loss.

Of the 60 juveniles that were considered to have dispersed outside the study area, 41 (68%) had moved unusually long distances (1.5–6.0 km) from their nest sites during the 10 days preceding the estimated date at which they left the study area (nine were subsequently located outside the study area). Of the remaining 19, three were also sub-

sequently located outside the study area. This suggests that the majority of juveniles that we lost track of did in fact disperse, rather than experience transmitter failure. Of the 40 found dead, 16 (40.0%) and 11 (27.5%) were eaten and presumably killed by raptors and mammals, respectively. A further 12 (30.0%) apparently died of starvation/exposure (six deaths occurred during a 2-day period of exceptionally cold, wet and windy weather in late May 2011), and a single (2.5%) bird was apparently killed by a car.

Thirteen of the 16 (81%) deaths attributed to raptors could not be attributed to a specific species. However, the remains of single juveniles and/or their radio transmitters were found in, or within 100 m of, peregrine (*Falco peregrinus*), kestrel (*F. tinnunculus*) and sparrowhawk (*Acccipiter nisus*) nests, respectively, strongly suggesting that these were the predators. None of the 11 deaths presumed to have been caused by mammals could be attributed to a specific species. However, a minimum of eight (73%) were likely killed by mustelids (stoats and weasels), because they were found in situations inaccessible to red fox, such as small holes or deep in boulder scree.

A similar proportion of early brood (14/76, 18%) and late brood (13/67, 19%) juveniles were apparently depredated ($\chi^2 = 0.02$, $p = 0.88$). During the first four days post-fledging, signs suggested that mammals were the main predator (5/6, 83%), with raptors being the main apparent predator thereafter (15/21, 71%). Mortality apparently from exposure occurred during the first eight days post-fledging, while the individual apparently killed by a car died approximately 3 weeks post-fledging.

Discussion

During 2011–12, we successfully provided supplementary food at 21 ouzel territories, with a further 34 territories classed as controls. However, none of adult provisioning rate to nestlings, fledging success, brood size at fledging, within-brood variation and individual nestling BCI at fledging, and post-fledging survival were positively associated with the provision of supplementary food. Post-fledging survival was positively associated with BCI at fledging, but there was no apparent association between BCI and the provision of supplementary food. Post-fledging mortality was apparently mainly due to predation by raptors and mustelid mammals. We therefore conclude that, during 2011–12, food supplementation did not improve the demographic rates which had previously been identified to be crucial for improving the population growth of ouzels in the UK. However, since the current and previous studies (e.g. Sim et al. 2011) have been carried out on areas with intensive predator control, these results may only be directly relevant to areas with similar levels of predator control.

Effects of food supplementation on provisioning rates

The majority of ouzel pairs that were supplied with supplementary food found it relatively quickly, usually within a day, and used it to feed themselves and/or their nestlings

in both years. Supplied food was mainly mealworms, which have been widely used to feed a number of passerine species due to their high protein and fat content, similarity to natural invertebrate food, and availability to receive in bulk at short notice (Bernard et al. 1997; Burfield 2002; Banjo et al. 2006). In this study, ouzel provisioning rate increased with nestling age as expected, and as noted for several other passerines (e.g. Goodbred and Holmes 1996; Zanette et al. 2000; Dawson et al. 2005). However, there was no evidence that food supplementation increased adult ouzel provisioning rate to nestlings, which suggests that natural invertebrate food was abundant in both years.

Effects of food supplementation on vital rates

Contrary to our predictions, we found no positive effect of food supplementation on ouzel fledging success, or brood size at fledging. These results are consistent with 9/19 (47.4%) of published studies on fledging success in small passerines, which found no positive effect of food supplementation (Robb et al. 2008). Although the provision of supplementary food resulted in increased brood size at fledging in great spotted woodpeckers (*Dendrocopos major*), it did not in great tits (*Parus major*), and brood size actually decreased in fed great and blue tits (*P. caeruleus*) in another study (Verboven et al. 2001; Harrison et al. 2010; Smith and Smith 2013).

None of our models predicting fledgling BCI successfully out-competed the intercept only model. In particular, supplementary fed individual ouzel nestlings fledged with a similar BCI to nestlings which received no supplementary food, in contrast to previous studies which indicated a positive effect of feeding on fledgling body mass (Arcese and Smith 1988; Simons and Martin 1990; Verboven et al. 2001). In this study, we found no decrease in within-brood variation in BCI in fed, as opposed to unfed, ouzel nestlings. As far as we are aware, no other studies have tested for potential effects of reducing within-brood variation in nestling BCI through the provision of supplementary food. Both these results indicate that there was no lack of invertebrate food sources for nestling ouzels.

Juvenile ouzels that fledged with a higher BCI had higher survival through the post-fledging period, a common (e.g. Yackel-Adams et al. 2006; Vitz and Rodewald 2011), though not universal (e.g. Anders et al. 1997; Kershner et al. 2004) finding in passerines. Recent work has suggested that the use of body mass alone may in some cases be a better measure of absolute body fat than indices adjusted for structural body size (Schamber et al. 2009; Labocha and Hayes 2012). In ring ouzels the adjustment for nestling body size (wing length) improved the regression of body mass on wing length^3, but only marginally (see Methods). We therefore conclude that our measure of nestling body condition was effectively a measure of body mass alone, and thus accurately reflects the key BCI parameter of nestling body fat content (Schamber et al. 2009; Labocha and Hayes 2012).

There was no positive effect of food supplementation on subsequent ouzel post-fledging survival, a result consistent with the only previous passerine studies which

have tested for this effect, in the New Zealand hihi (Armstrong et al. 2007; Walker et al. 2013). In addition, we found no positive effect of food supplementation on return rate in the year following ringing in ouzels, a result consistent with that in song sparrows (*Melospiza melodia*; Arcese and Smith 1988).

Causes and timing of mortality

Mortality rates of juvenile ouzels were considerably lower during 2011–12 than those during a similar study in the same study area during 2006–08, with most deaths apparently due to predation in both time periods (Sim et al. 2013b). Far fewer juveniles with known fates were apparently predated by raptors during 2011–12 (16/100; 16%) than during 2006–08 (42/103; 41%; $\chi^2 = 15.26$, $p < 0.0001$). However, the proportion of juveniles that were apparently predated by mammals did not differ between 2011–12 (11/100; 11%) and 2006–08 (19/103; 18%; $\chi^2 = 2.23$, $p = 0.14$). Precise identity of these apparent predators was known for only a small number of individuals, but no definite predation events by buzzards (*Buteo buteo*) were noted in 2011–12, in contrast to eight assumed predation events by buzzards in 2006–08 (Sim et al. 2013b). Similar numbers of buzzards attempted to breed in the study area in both time periods (pers. obs.), so this difference was not down to lower buzzard numbers. It seems likely that alternate buzzard prey [e.g. rabbits (*Oryctolagus cuniculus*) and voles (*Microtus* sp.)] were more abundant during 2011–12 than 2006–08, resulting in fewer ouzels being taken as prey during 2011–12. As in 2006–08, mammals predated most juveniles during the first four days post-fledging, with raptors being the main predators thereafter (Sim et al. 2013b).

Conclusions

Contrary to our predictions, the provision of supplementary food had no positive effect on adult provisioning rates to nestlings, fledging success, brood size, individual BCI at fledging, or subsequent post-fledging survival, and did not decrease within-brood variation in nestling BCI in ouzels. We therefore conclude that the supply of invertebrate food sources for nestlings was not a major limiting factor in our study area during 2011–12. However, it is possible that invertebrate food sources were unusually abundant during the two-year study period, in which case the provision of supplementary food would not be expected to create a positive effect on reproductive success or juvenile survival. Most feeding experiments, including this one, are short-term in nature and may therefore fail to detect potential positive effects on population demographics of providing supplementary food in years of natural food shortage (Robb et al. 2008). Thus, an experiment which was carried out over a longer time period, and at a larger scale, than the present one may have detected positive effects of the provision of supplementary food.

It remains entirely possible that factors acting on the migration routes and/or in the wintering grounds are important in driving observed declines in ouzel numbers

in the UK, and further work is required to investigate these (Sim et al. 2010). However, in the short-term, the provision of appropriate habitat mosaics on the breeding grounds is likely to be beneficial for the conservation of ouzel populations (Burfield 2002; Sim et al. 2013a). Further studies are required to quantify the precise mix of these habitat types, at the appropriate scale, which provide concealment from predators and access to abundant food supplies throughout the spring and summer months. The provision of such a complex habitat mosaic is thus likely to be of importance in reversing long-term ouzel population declines in the UK.

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Supplementary material 1

Supplementary Information

Authors: Innes M.W. Sim, Nicholas I. Wilkinson, Davide Scridel, David Anderson, Staffan Roos

Data type: species data

Explanation note: Details of the models predicting adult ring ouzel provisioning rate to nestlings, fledging success, brood size at fledging in successful nests, nestling BCI at fledging, within-brood variation in nestling BCI at fledging, and juvenile survival probability for up to 100 days post-fledging.

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